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THE INFLUENCE OF THE MUTATIONS OF THE PLEISTOCENE LAKES UPON THE PRESENT DISTRIBUTION OF CICINDELA.

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WITH the propagation of the late theories of life-zones founded upon temperature conditions, has come about a neglect of those considerations, of a more obscure though not less important nature, which we must recognize if we are to attain anything more than a superficial understanding of geographical distribution. The zonal theory as expounded by some of its more steadfast adherents has the apparent advantage of simplicity and moreover appeals directly to the 'practical man' since it is without doubt correctly assumed that most of our cultivated plants as well as numerous wild ones are limited to certain belts which are more or less closely coincident with the isotherms. The theory works well with agriculture in general, but it only imperfectly expresses the truth if we apply it to the natural distribution of Coleoptera on this continent. By natural, I mean original, in the sense of not being modified through the agency of civilized man; for cultivation and settlement have been potent factors in changing the range of numerous species, often resulting in the rapid extermination of the most characteristic types of a district and their replacement by others. Barriers which a few years ago were amply sufficient to prevent the intermingling of life of two nearby regions become no longer effective and the Faunæ and the Floræ become contaminated by the encroachment of strangers. Irrigation changes the nature of entire counties, lakes are drained, mountains are denuded of their forests and can no longer support the life which has been theirs for thousands of quiet years.

While it has been known for many years that the geological history of a given region has exercised a profound influence upon the present Fauna and Flora; while the effects of the Glacial

Epoch upon the life of this and other countries have long been recognized and carefully studied so that numerous distributional phenomena due thereto have thus been referred to their proper cause; and although modern lines of insect migration are being mapped and their relative importance determined, there is nevertheless a vast amount of detail to be worked out in order that certain local problems may be understood. It is with one of these local problems that we have now to do.

Some years ago, as the result of several seasons' collecting in the Great Basin, I became convinced that the distribution of certain species of Coleoptera therein occurring could not be accounted for by the theory of zonal arrangement of life, but apparently had as ultimate cause some condition or combination of conditions which belonged to the geological rather than the present history of the area under discussion. With the aim of testing this belief, further collections were made and all available data bearing upon the matter were collated, in order that it might be seen whether or not the above conclusion rested upon tangible grounds.

The Great Basin is a vast area of interior drainage, lying between the Wasatch Mountains and the Sierra Nevadas. The climate is arid, the soil in general desert, the vegetation such as characterizes regions of like nature in other parts of the world, being marked by the preponderance of a few species of dry dwarfed shrubs and the absence of forests except on certain higher mountain ranges which ridge the basin here and there. Since none of the rivers rising within the basin empty into bodies of water outside the limits, one of the most common methods of introduction of extra-limital species — by migration along the line of a water-course — is eliminated, and the fauna is not exposed to this source of modification. The two great mountain chains which form the eastern and western rims have acted as barriers to free interchange of inhabitants with the districts lying beyond, though some have doubtless crossed the passes from time to time. The southern boundary is less abruptly limited, so that those species which are suited to desert tracts may readily enter from that quarter, while the northern rim is made up of the series of hills that mark the divide between the Great Basin and the Columbia River drainage system.

We have here, then, a great enclosed region which, though comparatively open to migrations from the north and south, is nearly closed against encroachment from the east and west except in those cases where man may be conceded to have been a factor. We should expect the more characteristic forms to show extensive north and south distribution or that they may be confined to the basin and the more accessible adjoining areas. Some species no doubt originated, as such, within the limits of the basin proper, and I believe that, in some cases at least, we can determine which these are. It is with certain forms of this nature — that is to say with true indigenes — that we have now to deal.

Two types of littoral beetles may be said to be very characteristic of the Great Basin and to be dependent upon the peculiar conditions that occur there in the way of saline and alkaline flats in connection with springs and lakes. These are the Cicindelæ of the *echo* type and the species or subspecies of Tanarthrus which belong with *T. salicola*. Neither of these genera is confined to the basin, Cicindela being of wide distribution and evidently of southern origin, while Tanarthrus is not known outside of the southwestern United States. Besides the forms of this latter genus described from the lake shores of the Great Basin, a few species of somewhat different aspect are known to occur in saline spots in California and Arizona. The species of Bembidium of the *henshawi* type have also, in my opinion, attained their present specific structures within the limits of the Great Basin and are not to be considered migrants from the outside. For the present, I prefer to leave out of the discussion all of those Coleoptera not directly connected with the existence of alkaline and saline lakes, since the problem of their dispersal or distribution is different, in some respects, from that concerning the littoral forms and needs a separate body.

I am prepared to go farther than the simple statement that we can correctly indicate certain species as having arisen, as such, within the limits of the Great Basin. I believe it is also possible to show that some of these have been inhabitants of the region for long periods of time, and that in the course of their existence they have been played upon by conditions which arose as the consequence of geological changes; that we can point out the modifications which have taken place in the species and, to a considerable extent, we can trace the geological phenomena which are the fundamental or underlying causes of the modifications. Of course not all species will be equally affected by changes in their environment, nor will the modifications necessarily be parallel. Minute differences in the organic structures of insects indicate a probable diversity of physiological characters, and varying physiological activities may well modify such details as patterns of coloration or even the colors themselves.

As an example of an insect which has, in all probability, had its range determined and its specific characters modified by a series of geological changes, the history of which is not too remote and therefore fairly well known, we may take that aggregate of forms of Cicindela described under the names *C. echo* Casey and *C. pseudosenilis* W. Horn. These are without doubt modifications of one type; in fact they are so closely related as to be separable only in series. They are also very close to *C. willistoni*, and are ranked as races thereof by Dr. Walther Horn. However, the exact status of these names, specific or subspecific, does not concern us at present; the fact remains that these forms are closely related and may well have come from a common stock. *Cicindela fulgida*, to which *willistoni* was formerly referred as a variety or race, is readily separable by the thickly haired front. It may perhaps be an older offspring of the same stem.

The ways in which the beetles differ from one another may be briefly outlined, in order that the reader may understand the relationships and the better appreciate the account of the variations of each. It must be borne in mind that the descriptions refer more especially to series of specimens than to individuals, unless definitely stated to the contrary.

Cicindela fulgida Say. Easily separated from the allied species by the front being thickly hairy. The color is usually more coppery red, though specimens occur at Lincoln, Nebraska, in which the ground color is nearly black. Markings moderate, rather narrow as a rule, the middle band not expanded along the margin (or but very slightly so), the humeral lunule very oblique behind. This species belongs especially to the broad strip of plains lying to the eastward of the Rocky Mountains. It is known from Wyoming, Colorado, Kansas, Nebraska and New Mexico, but has not been reported from Central America nor from Old Mexico.[1]

Cicindela willistoni Leconte. A little stouter than *C. fulgida*, the color much less metallic. The front is sparsely haired; these hairs are readily lost, but the group of large punctures from which they spring may always be made out with little difficulty. Markings broader, the humeral lunule and median band always united along the margin; the apical lunule, also, usually, but not always, connected on the outer edge with the expanded marginal portion of the middle band. The tip of the humeral lunule (in those specimens in which it is free) is much less oblique than in *C. fulgida*. This insect is known only from the beaches of small lakes near Medicine Bow, Wyoming, where it was taken first by Dr. Williston, next by Mr. Warren Knaus and lastly by myself. I am not certain which of the little lakes was visited by Dr. Williston. He gives the locality Como Lake, but the usage of the village is not uniform and it may have been any one of three small lakes which lie within about twenty miles of one another. Mr. Knaus and I visited the one near the old station of Aurora, now several miles from the track. He calls it Como Lake,[2] while I have followed the prevailing custom of the villagers in speaking of it as Aurora Lake.

Cicindela echo Casey. Form of body nearly that of *C. willistoni*. Color brownish with an obscure purplish or coppery overcast. Front very sparsely hairy, the hairs being so readily removed that most specimens show only the punctures whence they originate. Markings usually rather narrow, the humeral lunule not or but slightly oblique at tip, middle band attaining the margin, usually but slightly dilated thereon but occasionally reaching the humeral lunule though not quite attaining the apical one which is complete. My series from Great Salt Lake (the original locality), most of which I collected at Saltair, in

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[1] It is not included in Dr. Walther Horn's List of the Cicindelidæ of Mexico, *Jour. N. Y. Ento. Soc.*, Vol. 11, p. 213.

[2] *Entomological News*, Vol. 13, p. 147.

June, shows quite a good deal of variation in the markings, the changes chiefly affecting the middle band. The marginal portion of this band is variously developed so that it may reach quite to the humeral lunule and almost to the apical one, or it may not be expanded at all. The discal part may be quite rectangularly or very obliquely bent near the middle and the terminal knob-like appendix may be abruptly formed and angularly bent from the stem or it may appear simply as an enlargement, without being noticeably deflected at all. A set from Humboldt Lake, Nevada, taken by myself in June, while not identical with the Saltair forms, shows a range of variations almost exactly corresponding thereto, all of the important features of the one being duplicated in the other.

On the shores of Honey Lake, near Amedee, California, I took a fine series of Cicindela which I refer, for convenience, to *C. echo*, though they are not typical. The form is nearly the same and the ground colors are about alike, but the Amedee specimens almost entirely lack metallic gloss and the surface sculpture of the elytra is notably shallower. The Amedee beetles also differ, as a species, from the Saltair specimens in the broader markings, the greater obliquity of the median band (the terminal knob less deflected), and in the expansion of this band along the margin so as to connect broadly with the humeral lunule. The apical lunule is free in all of my specimens. One individual is entirely blackish, except that each elytron bears two small spots, one of which represents the anterior portion of the humeral lunule, the other the posterior part of the apical.

Cicindela pseudosenilis Walther Horn. Green, shining, a few varying to brownish or reddish. Form of body as in *C. echo*. Front of head sparsely hairy. The elytral markings are very close to those of the Saltair *echo*; the middle band does not show a distinct tendency to spread along the margin in any of my specimens, so that it is not connected with nor closely approximated by the apical and humeral lunules. The chief variations are those exhibited in the descending portion of the middle band, for though this band is usually rectangularly bent the terminal knob shows numerous modifications. In some specimens this knob is largely developed though not hooklike, in others it disappears entirely, so that the descending part of the band is of nearly uniform size to the tip. None of the specimens in my series show a strong tendency towards the *willistoni* type of marking, the lead to that form going through *C. echo*. But some of the *pseudosenilis* approximate the Saltair *C. echo* so closely that if they were mixed they could scarcely be separated again. The shores of Owens Lake, in southeastern California, are the only definitely known haunts of the true *C. pseudosenilis*, though Dr. Howard writes me that in the National Museum is a single specimen said to have been taken by Mr. Coquillet in Los Angeles County — not very far distant. None of the other Californian collectors have found it in this latter locality, however. I found it in great abundance about the overflow of a spring on the upper beaches of Owens Lake, but none occurred in the immediate vicinity of the bitter waters of the lake itself.

Now that the variations of the insects have been described, we must turn again to the geological records and see what can be said of the early conditions of the country they inhabit. The geology of the Great Basin has been worked out by Dr. G. K. Gilbert,[1] and Dr. Israel C. Russell,[2] the results of their labors appearing in two fine volumes from which the main geological items used in this discussion are compiled. We find that in the early Pleistocene the basin held two great freshwater lakes: Bonneville, covering the greater part of western Utah and a small portion of eastern Nevada and southern Idaho, and Lahontan, occupying an extensive area in western Nevada and eastern California. Between them lay a broad plateau or divide, forming a watershed, the hydrographic basins of the lakes being contiguous. Both of these lakes were of irregular shape, Lahontan being especially so, with numerous arms and bays extending up narrow, flooded valleys. Each lake had two great periods of high water, which had been preceded by times of drought and desiccation, the second stage of flood being higher than the first. These times of plenty correspond to the two glacial epochs of the Sierra Nevadas, though the climate is supposed to have been only moderately humid and rather cold. The increase in the size of the lakes is not ascribed to the melting of the glaciers, though this must have added considerably to their volume, as the ice cap was not large enough to furnish so much water. While Lake Lahontan seems not to have overflowed, Lake Bonneville broke through the barrier to the north and found an outlet to the sea by way of the Columbia River basin.[1] The desiccation of the lakes during the dry times is thought to have been more complete than at present.

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[1] *Lake Bonneville.* Monographs of the U. S. Geological Survey, I, 1890.

[2] *Geological History of Lake Lahontan.* Monographs of the U. S. Geological Survey, XI, 1885.

The relation of our modern lakes to those of Pleistocene times is principally that of occupying the same area; that is to say, the bodies of water now existent have, in the main, been formed since the old lakes dried up, and are not to be considered remnants left by incomplete evaporation, since in the latter case the waters must have been much salter than they are. An exception may perhaps be made of Great Salt Lake, the evidence being inconclusive; and I have no data of this nature concerning Owens Lake and Mono Lake, which never formed part of these two larger bodies, but were separate even during the high-water periods of the Pleistocene. The littoral Fauna may easily have been preserved, even through times of great drought, by clustering about the edges of springs. In this way, even to-day, we know that some are carried over; for example, this very *Cicindela echo* flocks on the damp ground in the vicinity of the little springs about the edge of the now dried-up Humboldt Lake. Many springs are of a far more permanent nature than the shallow lakes into which they discharge, and I think that we may safely assume that they lasted, in many instances, through the times of most complete desiccation.

Now let us consider the relation of existing lakes (which have been examined for material for this paper), and those of ancient times, in order to see what opportunity the beetles have had for differentiation through isolation. I have visited Great Salt Lake, Utah Lake, Humboldt Lake, Honey Lake, Walker Lake,

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[1] This may possibly account for the present occurrence in the Columbia district of such widely distributed Great Basin species as *Cicindela hæmorrhagica* and *Saprinus estriatus*.

Owens Lake and Mono Lake, and found *Cicindela echo* or *C. pseudosenilis* at all but three — namely, Utah, Mono and Walker. I cannot definitely assert that the species, in some of its forms, is absent from all of these three, but we have no evidence to show that it occurs there. Mono Lake may perhaps lie at too great an altitude for the insect to flourish, or it may never have been introduced into the district. It is possible that a more extended search may yet disclose some form of it there, my visit having been a hurried one and productive of no Cicindela whatever, though *C. pseudosenilis* and *C. hæmorrhagica* must have been flying in abundance at Owens Lake, distant about a hundred miles. Walker Lake has been twice visited by me with the special object of looking for some form of *C. echo*, but I took only *C. hæmorrhagica* and a variety of *C. oregona*, both in plenty. I hope that if any entomologist has the opportunity, he will visit the flats at the upper end of the lake, in the vicinity of the mouth of the river, since I have noticed that the colonies are sometimes confined to a limited area and may easily be missed. It will be well also to examine the neighborhood of the large spring said to exist near Wabuska; it dates back to considerable antiquity and may yield something interesting. Utah Lake has been visited by several entomologists at different times, and it seems that if *C. echo* occurs there it should have been met with before this.

These three lakes which have failed to yield material after exploration may be left out of the rest of the discussion. Of those which have been productive, Owens Lake has been distinct for a vast period, having, as we have seen, been separate even during the greatest extension of the others. Great Salt Lake was a part of Bonneville, while Humboldt Lake and Honey Lake lie in the ancient bed of Lahontan. The small bodies of water in Wyoming, which harbor *C. willistoni* were of course not included in either and had no communication therewith.

Looking again at the beetles, we find:

(a) The Owens Lake form, which has probably been isolated since (at least) early Pleistocene times, is sufficiently well differentiated to have been separated by systematists as a distinct species, though this view is no longer held.

(b) The form from Honey Lake, on the extreme western border of the old Lake Lahontan, is also well differentiated, though not in the same way. This lake is extremely shallow and evanescent, having dried up at least twice within the memory of the present generation, and has no doubt been separated from the main body of the old lake since a comparatively early period in the second great decline in size of the latter. The beetles live about the seepage on the lake beach that comes from the hot springs a few hundred yards distant. While it is impossible at present to point out the details which lead to variation in any one direction, it is evident that local conditions, aided by long isolation, have so modified this form that it is now readily separable, in series, from those taken elsewhere.

(c) The specimens from Humboldt Lake, farther to the east, are more of the type of typical *echo*, differing but little from the series taken at Great Salt Lake, Utah, whence the species was originally described. While the Humboldt colony must have been separate from the latter for a great length of time, it has been comparatively little differentiated therefrom. The reason for this cannot now be assigned. It may be that the local conditions requisite to incite variation were not present, or perhaps the two colonies have simply varied along parallel lines. Though isolation is unquestionably favorable to differentiation, it does not follow that every isolated colony must differ from every other. It is well known that with certain species of Cicindela some colonies produce mostly specimens of one type, others will produce those of another, while a third will be composed of a mixture of both, with all the intergrades.

(d) The form from Great Salt Lake, to which the name *C. echo* is properly applied, is not like that from Owens Lake nor that from Honey Lake, though closely approached by the specimens from Humboldt Lake.

(e) On the shores of the small lakes in Wyoming, we have *C. willistoni*, a closely related form occurring (as far as we know) nowhere else, which according to geological evidence can scarcely have had any communication with the Great Basin colonies during Pleistocene times. I am inclined to look to a still more remote date for the cause of this phenomenon, and consider *C. willistoni* a survivor of an early stock which, during the Tertiary period, inhabited the present Rocky Mountain region and in all probability the adjacent districts to the east and west at the time of the great extension of the Tertiary lakes. *C. willistoni* is much better differentiated from the races of *C. echo* than those races are among themselves.

My conclusions are these: That in *C. echo* (with its several races, including *C. pseudosenilis*) and *C. willistoni*, we have two branches of a stem which were probably separated by some of the orographic movements which gave rise to the upheaval of the Wasatch and Rocky Mountains. That this stem form was a littoral species and the branch remaining in the Great Basin was carried over the interval between the dissolution of the Tertiary lakes and the appearance of the great Pleistocene lakes by clinging to the borders of springs and other bodies of water. That with the growth of Lake Bonneville and Lake Lahontan and the contemporaneous filling by water of the smaller basins, it spread over the whole habitable area between the Wasatch and the Sierras. The subsequent desiccation of the greater part of the Lahontan and Bonneville basins left a series of smaller lakes of varying permanence and more or less complete isolation. Local conditions, acting on the members of colonies of the beetles thus separated from their neighbors, have given rise to variations of different kinds and certain of these variations have been preserved and accentuated through this isolation. As a consequence, we have the phenomenon of local races, strongly or slightly marked according to the strength of the conditions exciting variability and to the comparative degree of isolation of the colony after a certain character had made its appearance. Owens Lake and Honey Lake, having been long since separate from the larger bodies and presumably subjected to different conditions, climatic and otherwise, because of their proximity to the Sierras, have at length produced upon their shores racial types which are easily distinguished from each other and from the forms found farther east.

If the species of Cicindela used in illustration were alone in presenting the general phenomena noticed, one might well doubt the sufficiency of the evidence adduced in support of the foregoing conclusions: and as the matter stands, I am well aware of the circumstantial nature of much of it and of the many possibilities of wrongly interpreting the facts. However, I have been collecting and studying other species of littoral Coleoptera in the Great Basin, with a view to further prosecution of the problem, and find much in corroboration. It is evident that the same general law is followed in the variations of Tanarthrus, and I hope also to demonstrate a parallelism in certain Carabidæ and Histeridæ which are associated with it.

State University of Iowa,
Iowa City, March 19, 1904.